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Nomenclatural and Systematic Problems Surrounding *Eterusia aedea* (Linnaeus, 1763) (Lepidoptera: Zygaenidae: Chalcosiinae)

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Shen-Horn Yen (2004) Nomenclatural and systematic problems surrounding *Eterusia aedea* (Linnaeus, 1763) (Lepidoptera: Zygaenidae: Chalcosiinae). *Zoological Studies* **43**(1): 20-34. Nomenclatural and systematic problems surrounding *Eterusia aedea* (Linnaeus, 1763), a polytypic species comprising 13 subspecies in the East Palaearctic and Oriental regions, were investigated. Until recently, the nominotypical "*aedea*" was interpreted as representative of populations from temperate China. However, Linnaeus had stated that India was the "type locality". Examination of Clerck's illustration on which Linnaeus' description was based reveals that true *aedea* is the color form *lepcha* Jordan, 1907, of *aedea edocla* (Doubleday, 1847), which ranges throughout North India to South China. I therefore suggest synonymizing *edocla* and its synonyms to *aedea* and redefining the concept of the latter. *Eterusia sinica* Ménétriés, 1857, long treated as a synonym of *aedea aedea*, is revived, newly combined with *aedea* and applied to populations from temperate China. The research histories and perspectives of this species are also discussed. http://www.sinica.edu.tw/zool/zoolstud/43.1/20.pdf

Key words: Wing pattern, Carolus Linnaeus, Carl Clerck, Typification, Tea pest.

Among the zygaenid subfamilies, the Chalcosiinae Walker, [1865] 1864 is a diverse group 2nd only in size to the Procridinae, and may exhibit the highest diversity in morphology and ecology within the superfamily Zygaenoidea and the non-obtectomeran apoditrysian Lepidoptera (Yen 2003b c). Owing to their brilliant coloration, high sexual dimorphism, complicated mimicry patterns, little-known biology, and rarity in museum collections, this group has received considerable attention from researchers and insect collectors, and their taxonomy has been very confusing since the 18th century. This subfamily currently comprises around 70 genera and 370-400 species (Bryk 1936, Tremewan 1973, Fletcher and Nye 1982, Endo and Kishida 1999, Yen 2003b c) and is widely distributed from Palaearctic East Asia, through Southeast Asia, to Papua New Guinea and its associated islands, but it is not yet known from Melanesia, Micronesia, or Australia. An isolated genus, *Aglaope* Latreille, 1809, comprising 2 sibling species restricted to southern Europe and North Africa (Morocco), demonstrates an intriguing biogeographical disjunction from all other relatives.

In contrast, unlike the western Palaearctic Zygaeninae (Burnet moths) and Procridinae (Forester moths and Smoky moths), which have been very well investigated in many aspects and well-illustrated in many works (e.g., Ebert 1994, Guenin 1997, Efetov and Tarmann 1999, Naumann et al. 1999, de Freina and Witt 2001), the majority of previous studies accumulated for the Chalcosiinae have been restricted to establishment of new taxa and faunistic surveys. Nearly all the genera recognized by the current authors were established before the 1940s, and only 5 genera have subsequently been added (Yen and Yang 1997 1998, Efetov 1999, Owada and Horie 2002a). Among the chalcosiine moths, the genus *Eterusia* Hope, 1841 (type-species: *Eterusia tricol-*

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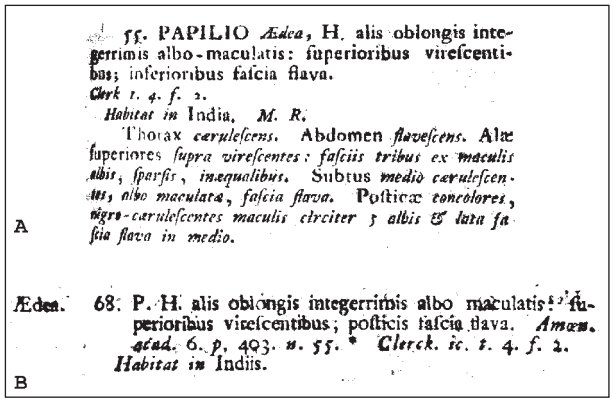
or Hope, 1841) is well-known for its great diversity in continental Asia and the Pacific Is., its sexual dimorphism and polymorphism, and its mimetic involvement with several different insect groups (Owada 1998b, Owada and Ta 2002). Current interests in *Eterusia* are focused on regional taxonomic revisions (Owada 1989 1992 1996 1998 2000 2001 2002, Yen and Yang 1998, Kishida and Endo 1999, Owada and Horie 1999 2002b, Horie et al. 2000, Yen 2003a), morphology (Fänger et al. 2002), and preliminary field observations on mimicry complex participation (Owada 1998b 2000, Nishihara 1999, Owada and Ta 2002). Due to the uncertain monophyly and chaotic taxonomy, Yen (2003c) "cleaned up" the genus by transferring several species to *Eusphalera* Jordan, 1907, and separating the remaining species into several species groups according to their wing patterns, copulatory structures, and scent organs. Results of genus-level phylogenetic analyses (Yen 2003c) have shown that the conventional concept of *Eterusia* is polyphyletic.

Of these *Eterusia* species, *E. aedea* (Linnaeus, 1763) is the most widely distributed species within the subfamily. It is highly differentiated into 13 subspecies ranging from the Indian subcontinent (including Sri Lanka), through Indochina, Tibet, China, and Taiwan to most island-groups of Japan (Owada 1989 1998a 2000 2001 2002). Several subspecies have been reported as occasional pests of tea trees (*Camellia* spp., Theaceae) in India (Maxwell-Lefroy 1909, Fletcher 1914 1920, Andrews and Tunstall 1915, Sevastopulo 1940 1947 1949, Robinson et al. 2001), Sri Lanka (Green 1898, Barlow 1900), Vietnam (Du Pasquier 1932), China (Zhu and Wang 1979, Wang 1987), and Taiwan (Sonan 1933, Guan and Yeh 1977, Nishihara 2001). During a cladistic study of the *Eterusia-Soritia* complex, I found that several systematic and nomenclatural problems surrounding the nominotypical *E. aedea* which have not been resolved. First of all, the authorship of *E. aedea*, originally described as a butterfly, namely "*Papilio* (*Heliconius*) *aedea*", has been misattributed to Carl Alexander Clerck (1710-1765) in various works (e.g., Bryk 1936, Tremewan 1973, Fletcher and Nye 1982, Owada 1989 1998 2001). Clerck was a Swedish entomologist and arachnologist, who figured many of Linnaeus' butterflies and worked closely with Linnaeus. Clerck's figures appear frequently to have been made from Linnaean specimens. The legends to Clerck's figures often cite the number given to that species by Linnaeus. Although they are not part of the name, these legends have often been misinterpreted as available descriptions of the species figured by Clerck. As already indicated by Honey and Scoble (2001: 291), the authorship of *Papilio* (*Heliconius*) *aedea* should be attributed to Linnaeus. The date of publication of *aedea*, erroneously given as 1759 by Bryk (1936) and various other authors, was discussed and corrected to 1763 by Tremewan (1973). Linnaeus (1763a) indicated that the type locality of *aedea* was "India" (as "Indiis" in Linnaeus 1767) (Fig. 1). Later nominotypical *aedea* was interpreted as originating from the North Indian population by Doubleday (1844), Cotes and Swinhoe (1887), Hampson (1892), Kirby (1892), Swinhoe (1892), and Fletcher (1925). Doubleday (1844) discussed differences between Linnaeus' *aedea* and his *edocla*, and also provided a wood-cut (Fig. 2B) of a specimen donated by Stainsforth from Sylhet. However, since Leech's (1898) study of the Chinese Lepidoptera, the name *aedea* has also been applied to populations in temperate China (Jordan 1907, Owada 1989, Endo and Kishida 1999). Therefore, the current taxonomic viewpoint (e.g., Owada 1989 2001, Endo and Kishida 1999), that treats the Chinese population as the nominotypical subspecies, and uses *edocla* (Doubleday, 1847) for subspecies from northeastern India through northern Indochina, to Southwest and South China, obviously do not correspond to Linnaeus' statement. As indicated by Honey and Scoble (2001), the great majority of Linnaeus' butterfly species (including *aedea* in Linnaeus's concept) have been



A

55. PAPILIO *Ædea*, H. alis oblongis integerrimis albo-maculatis: superioribus virescentibus; inferioribus fascia flava.
Clerk t. 4. f. 2.
Habitat in India. *M. R.*
Thorax *cæruleſcens*. Abdomen *flaveſcens*. Alæ superiores *ſupra virescentes: ſaſciis tribus ex maculis albis, ſparſis, inæqualibus*. Subtus *medio cæruleſcentes, albo maculatæ, ſaſcia flava*. Poſticæ *concolores, nigro-cæruleſcentes maculis circiter 3 albis & lata ſaſcia flava in medio*.

B

Ædea. 68. P. H. alis oblongis integerrimis albo maculatis: superioribus virescentibus; posticis fascia flava. *Amœn. acad. 6. p. 403. n. 55.* * *Clerck. ic. t. 4. f. 2.*
Habitat in Indiis.

Fig. 1. Original description of *Papilio* (*Heliconius*) *aedea*. A. Linnaeus (1763a) described this species based on Clerck's illustration (see Fig. 2) and inferred that India was the type locality; B. Linnaeus (1767) in *Systema Naturae* mentioned this species again and cited *Centuria Insectorum* in the series *Amoenitates Academicae* (1763b). Here he used "Indiis" as the collection site of *aedea*.

divided into subspecies. This has increased the difficulties in evaluating the identities of Linnaeus' species, because very few of Linnaeus' type localities are specific: most are extremely broad (e.g., "Indiis", which could mean East Asia or the Caribbean Is. or even, perhaps tropical areas more generally); and several are inaccurate. When I examined the illustration of "*Papilio* (*Heliconius*) *aedea*" in Clerck's *Icones* in the BMNH library (Fig. 2A), I found that the figure does not match the current concept of *aedea* which is based on temperate Chinese material, but resembles the female of the color form *lepcha* Jordan, 1907 of *aedea edocla*, and also *aedea okinawana* Matsumura, 1931 from Yaeyama I. of Japan and *aedea formosana* Jordan, 1907 from Taiwan.

One of the principles of the international rules of zoological nomenclature is to promote stability among scientific names. Especially for an agriculturally important species, it is desirable to revise the taxonomic identity by sourcing the original literature and collections and to fix the use of names. Therefore the aims of the present study were to answer the following questions: (1) Does the specimen on which Clerck's figure was based still survive, and can it be used to justify the identity of the nominotypical *aedea*? (2) If it does not, how do we evaluate the actual status of the Linnaean *aedea* and link modern material to the currently accepted concepts of available names? (3) Do wing patterns and wing size provide reliable characters to distinguish the continental subspecies of *E. aedea*? (4) Are the temperate Chinese and the Indian-Indochinese populations distinguishable from each other? (5) Is there any clear geographical boundary between them? I hope the results of the present study not only serve to stabilize the use of *aedea*, which is agriculturally important in Asia, but also to provide an applicable protocol to verify the taxonomic status of a polytypic species described in the Linnaean period.

MATERIALS AND METHODS

Examination of historical collections and associated literature

The names published by Carl Linnaeus are among the oldest names in the Lepidoptera and are some of the most important. Robinson and Nielsen (1983) revised both Linnaeus' and Clerck's names of the Microlepidoptera; Mikkola (1985) revised the European species of Geometroidea and Noctuoidea described by Clerck; Mikkola and Honey (1993) revised

Fig. 2. Illustrations of the nominotypical *Eterusia aedea*. A. The original illustrations from Clerck's *Icones* showing the underside and upperside of a female from "India"; B. a wood-cut of a female specimen from Sylhet (Bangladesh) shown by Doubleday (1844).

Linnaeus' Noctuoidea; and recently Honey and Scoble (2001) revised the "butterflies" described by Linnaeus. The works of Linnaeus and the history and recuration of his collection have been recounted in detail by Jackson (1890), Day and Fitton (1978), Robinson and Nielsen (1983), and Honey and Scoble (2001), and will not be repeated here. I attempted to search for the specimen on which Clerck's figure was based from the following key collections and institutions and from photographs taken from these collections by the courtesy of the curators: the Fabricius Collection (Zoological Museum, Copenhagen), the Charles De Geer and Carl Clerck Collection (Naturhistoriska Riksmuseet, Stockholm), Gyllenhaal Collection and Queen Ludovica Ulrica Collection (both housed at the Museum of Evolution-Zoology, The University of Uppsala, Sweden), and the Linnaean Collection (The Linnaean Society of London). The following literature was also consulted to trace the history of the recuration of the Linnaeus collection: Kirby (1870), Aurivillius (1882), and Wallin (1994). For the history of each collection see Honey and Scoble (2001).

Examination of modern collections

In addition to historical collections and literature, I also compared all the type specimens (or their original descriptions) and modern specimens of the taxa included in the current concept of "*aedea*" (see Appendix 1). Material from the following institutions was examined: BMNH (The Natural History Museum, London, UK), DEI (Deutsches Entomologisches Institut, Eberswalde, Germany), ELKU (Entomological Laboratory of Kyushu University, Fukuoka, Japan), HUFA (Hokkaido University, Faculty of Agriculture, Sapporo, Japan), NSMT (National Science Museum, Tokyo, Japan), ZIN (Zoological Museum, Zoological Institution of Russian Academy of Sciences, St. Petersburg, Russia), and ZMHB (Zoologisches Museum für Naturkunde, Humboldt University, Berlin, Germany). Because the copulatory structures of both sexes of this species do not significantly differ between subspecies (see Owada 1989: figs. 21-33), I particularly focused on variations and consistency of the female wing pattern among specimens from various geographical sources. I also compared wing pattern and sizes of both sexes from various provinces of temperate China and those from northeastern India, Bangladesh, Burma, Thailand, Vietnam, and South China.

RESULTS

Does the "type specimen" of "*Papilio* (*Heliconius*) *aedea*" still survive?

All my efforts failed to locate the specimen on which the figure in Clerck's *Icones* was based. The specimen is presumably preserved in one of the above institutions linked to Linnaean material. However, since Kirby's (1880) and Aurivillius' (1882) catalogues, there has been no record of the specimen of "*Papilio* (*Heliconius*) *aedea*" . In the latest version of the catalogue of Linnaean specimens housed at Uppsala University Zoological Museum (Wallin 1994), there is also no record of this specimen. I also examined the *E. aedea* specimens in those collections, but none of them seems to be the specimen illustrated by Clerck.

The source of Linnaean specimens

Because the features of the moth illustrated by Clerck can be seen not only in material from northern India, but also in specimens from Yaeyama Island and Taiwan, an issue to be clarified is if Linnaeus's "India" or "Indiis" actually meant a broad geographical range in the Oriental Region. Or could Linnaeus have received material from Yaeyama I. or Taiwan during that period? The origin of much of the Linnaean material is still unknown. Honey and Scoble (2001) provided comments on the notable sources. Among the sources discussed by Honey and Scoble, only the material from China and Java supplied by Peter Osbeck (1723-1805) provides a possible origin relevant to *aedea*. Osbeck was a student of Linnaeus and a minister in the Lutheran Church. He obtained specimens while acting as ship's chaplain on a voyage to the East Indies with the Swedish East India Company (1750-1752). Osbeck published an account of his voyage in 1757. He later revised the account, which was published in German (Osbeck 1765). According to his diary, his journey was around Hong Kong and southern Guangdong (=Kanton, Canton, Kwangtung) Prov., China, where he described some insects (e.g., fireflies). However, he mentioned no moth species, nor did Linnaeus mention his name in the description of *aedea*.

I next tried tracing the history and possible origins of Linnaeus' botanical specimens. It has been inferred that traders of The Dutch East India Company (Vereenigde Oost-Indische Compagnie (VOC) or the United Dutch East India Company),

formed in 1602, to manage their colonial businesses and trade, might have been suppliers of material from the region comprising Japan, the Ryukyus, Taiwan, and China (Tanaka 1995). Evidence that the VOC might have been suppliers of botanical material from the Japanese mainland to European naturalists has been discussed previously (Nicolson et al. 1988, Nordenstam 1993, Wallin 1993, Hinz 2001). The Linnaean Correspondence, in a database produced by Jacobson et al. since 1998, also corroborates that Linnaeus had frequent contacts with traders of the VOC and also the Swedish East India Company. However, there is no evidence that Linnaeus received material from the Yaeyama Is. or Taiwan during the middle of the 18th century; on the contrary, no Linnaean species was described from the Ryukyus, where species endemism is high, and the activities of the VOC in Taiwan ended by 1662 (Lin 1997), almost 100 years before Linnaeus described *aedea*. Considering all these together, I consider that "India" is more likely the source of the specimen illustrated by Clerck.

Comparison of Clerck's figure and modern specimens

Having compared modern collections with Clerck's illustrations of other lepidopteran species (see also Honey and Scoble 2001: figs. 37-39), I consider that the colors and techniques used in his illustrations are reliable and precise enough for judgments of taxonomic status.

I conducted a comparison of female wing patterns based on modern specimens from various institutions (see Appendix 2). I particularly focused on the 3 subspecies (Indian-Indochinese, Chinese, and Yaeyama's) involved in these problems, plus *formosana*, the Taiwanese endemic, because Owada (1989) suspected that *formosana* was mostly allied to the subspecies of the Yaeyama Islands.

The drawing of Clerck's "*aedea*" (Fig. 2A) is characterized by the following features: (1) ground color of forewing dark green; (2) forewing underside with antemedial zone forming a continuous broad band; (3) 4 large submarginal white spots present on cells m3, cua1, cua2, and 1a of hindwing, each spot bordered by metallic blue veins; (4) marginal to submarginal zone metallic blue; (5) postmedial cell spot separated from other submarginal ones and concolorous with interior sections of M1 and M2; and (6) base of hindwing metallic blue. Among the 13 subspecies, only the females of the *lepcha* form of *edocla* (Fig. 3A, B, see also Endo and Kishida 1999: 61, fig. 9), *okinawana* (Fig. 3I), and *formosana* (Endo and Kishida 1999: 61, fig. 12) match the general pattern of the illustration, while none of the examined specimens from temperate China (Fig. 3K) have a greenish forewing or hindwing with a submarginal metallic blue sheen. Compared with Clerck's illustration, the green color of the forewing of *okinawana* has more sheen and higher brightness, and the submarginal blue sheen on the hindwing underside is much weaker. The features of *okinawana* are partly shared by the subspecies *masatakasatoi* Owada, 2001 (Owada 2001: figs. 11, 12) from Nakanoshima I. but its hindwing base is blacker with very little bluish sheen, and the hindwing submarginal blue zone is narrower. The female *formosana* from Taiwan is extremely similar to the *lepcha* form of *edocla* and occasionally has dark green forewings. But, in general, the ground color of *formosana* is dark brown with a slight greenish sheen, while the hindwing base is rather dark and less developed than that of *edocla*. The feature of the 4 submarginal white hindwing spots is present in *edocla* (form *lepcha*), *okinawana*, *formosana*, and the northern, eastern, central, and western Chinese populations. However, these spots in the northern, central, and eastern Chinese populations (Fig. 3K) are more developed than in any other subspecies or in the specimen illustrated by Clerck. The above discussion shows that only the female of the *lepcha* form of *edocla* (Fig. 3A-C) from northeastern India matches Clerck's illustration, and neither *okinawana*, *formosana*, nor the current concept of *aedea* from temperate China match the features demonstrated by the illustration. Consequently, 2 nomenclatural treatments should accordingly be proposed.

Taxonomic treatment and typification

The above discussion has clarified that the nominotypical *aedea*, based on Clerck's illustration, should be redefined to represent one of the color forms of the polymorphic Indian-Indochinese populations. All names proposed for different color forms of *aedea* from this region, e.g., *edocla* Doubleday 1844 (figs. D-F), *dulcis* Butler 1881 (figs. D-F), *signata* Möschler 1872 (figs. D-F), *magnifica* Butler 1879 (figs. G, H), and *lepcha* Jordan 1907 (figs. A-C), should be synonymized with *aedea*. Since the nominotypical *aedea* is no longer applicable to populations from temperate China (northern, eastern, central, and western),

Fig. 3. Color forms of *Eterusia aedea* subspecies from various areas. Left: underside; right: upperside. A-H. *E. a. aedea*: A. ♀, Khasia Hills (India); B. ♀, Darjeeling (India); C. ♀, Shillong (India); D. ♀, Khasia Hills (India); E. ♀, Khasia Hills (India); F. ♂, Assam (India); G. ♀, Buxa (Bhutan); H. ♂, Assam (India). I. *E. a. okinawana*, ♀, Ishigaki Island (Japan). J-N. *E. a. sinica*: J. ♀, Guizhou (China); K. ♀, Zhoushan Islands, Zhejiang (China); L. ♂, Jiujiang, Jiangxi (China); M. ♂, Wenzhou, Zhejiang (China); N. ♂, Tatsienlu, W. Sichuan (China).

Eterusia sinica Ménétriés, 1857, previously synonymized with *aedea* (Bryk 1936), appears to be a potentially valid name for these populations. I attempted to look for Ménétriés' type specimen, which is presumably still deposited in ZIN in St. Petersburg. However, I failed to locate any Chinese specimens of *Eterusia* in ZIN so the identity of *sinica* can only be inferred from the original description and the taxonomic histories of the other species described by Ménétriés. In his paper in 1857, Ménétriés described "macromoths" and butterflies from North China. Judging from the present distribution of the other species described by him, the geographical source of his *sinica* is more likely North China rather than the South or Southwest, where nominotypical *aedea* is distributed. Therefore, I consider that Ménétriés' name *sinica* can be applied to these populations although the type has not been found. Examination of materials from northern, eastern, central, and western China (see Appendix 2) also reveals that populations in these regions, called *sinica* hereafter, bear the following characters that consistently differ and are distinguishable from the *lepcha* form of *aedea*: (1) *sinica* (forewing length, 29.8 ± 0.09 mm (male, *n* = 20); 32.14 ± 0.06 mm (female, *n* = 20)) is much smaller than *aedea* (forewing length, 33.32 ± 0.24 mm (male, *n* = 20); 35.21 ± 0.13 mm (female, *n* = 20)); (2) the forewing submarginal white patches on cua1, cua2, and 1a are longer and more developed in both sexes of *sinica*; (3) the forewing antemedial white patches of *sinica* are longer than 1/5 of cell 1a, but this feature is inconsistent in *aedea*; (4) no black form has been observed in *sinica*, but black forms are very common in *aedea*, and the pre-sence of this form is not correlated with geographical distribution; and (5) the submarginal dark blue metallic sheen in *sinica* is very weak, but more developed in *edocla*. The genitalia and the associated abdominal segments of both sexes show no significant differences between *sinica* and *aedea*.

Additionally, during this study, the status of *Heterusia aedea* var. *septentrionicola* C. et R. Felder, 1862, was reviewed. This "variety" name has not been used nor has the material been examined since its description. Cajetan von Felder (1814-1894) and Rudolf Felder (1842-1871) described it in their paper dealing with the Lepidoptera from central China (Shanghai, Jiangsu, and Zhejiang Provs.) and Japan. Interestingly, they indicated that neither China nor Japan was the source of the material of *septentrionicola*, but Sri Lanka (as "*ceylanicis*"). I found 3 specimens of *E. aedea* in the BMNH, bearing typical Felder collection labels, and matching Moore's *cingala*, which was described from Sri Lanka in 1877. So this name is indeed not applicable to any of the Chinese populations. However, as *septentrionicola* has never been used or catalogued since it was described, and in order to maintain the nomenclatural stability of an important tea pest in Sri Lanka, the priority of *septentrionicola* should be suppressed under ICZN Code Article 23.9 to preserve the current use of *cingala*. An application to conserve usage of *cingala* will be proposed in a separate paper to the International Commission on Zoological Nomenclature (Yen, in press).

A critical issue arising from the above taxonomic treatments is whether any typification should be proposed for *aedea* or *sinica*. Honey and Scoble (2001) recommended that designation of lectotypes or neotypes for historical material should not be encouraged if there is little reason to doubt the modern identity of the species in question. In the case of "*aedea*" although interpretations of Linnaeus' *aedea* have been historically chaotic and the original specimen seems to be missing, Clerck's illustration exhibits precise evidence from which the judgment for *aedea*'s true identity can be inferred. Additionally, the conventional policy for designation of a neotype of a Linnaean species is to select a specimen from the Linnaean Collection or related collections. Since I did not locate any specimen of *E. aedea* in any of the relevant historical collections, I decided to leave the typification issue to future studies. As to Ménétriés' *sinica*, although the potential type specimen has not been located in ZIN, St. Petersburg, I prefer not to designate a neotype in the present study because his description of *sinica* was clearly based on material from North China, where only 1 "subspecies" is present.

DISCUSSION

Do *aedea* and *sinica* have a clear geographical boundary?

Endo and Kishida (1999) gave a distribution map of these 2 subspecies (as *edocla* and *aedea*). They considered that *aedea* ranged from the East Himalayas, including eastern Tibet, to South China, and *sinica* from the Shandong Peninsula southeast to Fujian Prov. and northwest to Gansu Prov. However, they were not sure about the exis-

tence of a geographical boundary, possibly starting from southern Guangdong Prov., extending northwest to Gansu Prov. and west to Nepal (Fig. 4). Difficulties in confirming geographical boundaries are due to insufficient material from different provinces of China and clinal variation between the 2 subspecies found in northern Guangxi and Guizhou Provs. (Fig. 3J). Material from Guangxi and Guizhou is similar in size to *aedea*, but the forewings have a more-developed dark-green or brownish-green sheen, which is more commonly seen in *aedea*. The frequency of yellow in the hindwing, a significant feature of the *magnifica* form (Fig. 3G, H) of *aedea*, is much higher than in material from other regions of China. Materials from Guangxi and Guizhou still maintain some features typical of *sinica*, however, such as more-elongate antemedial white patches in the forewing, and a very weak blue sheen of the hindwing submarginal zone. Such features can also be observed in specimens from northern Vietnam (Owada 2001: fig. 43). Endo and Kishida also included Tibet in the range of *aedea*, but examination of Tibetan material (Fig. 3N) in the BMNH suggests that Tibetan populations should be classified as *sinica* by their smaller size, narrower forewings, and lack of a dark-green sheen or brown ground color in the forewing. In future studies, it would be desirable to investigate if these 2 subspecies have a clear geographical segregation, and if they have formed a hybridization zone in southwestern China and the area between Tibet and Nepal.

Which subspecies are pests of tea?

Eterusia aedea has been repeatedly reported as a "defoliating" pest of tea from different areas. However, literature records are not necessarily based on scientific monitoring or detailed biological research, and many of the records can possibly be traced back to a single source. Although host plant records and immature biology of all 13 subspecies are known, only a few results have been formally documented (e.g., Sonan 1933, Okuno 1952, Zhu et al. 1979, Nishihara 1992 1995 2001, Murase 1993 1995, Owada 1995). Appendix 3 provides a list of host plant records of this species, covering 18 plant species in 13 genera, 11 families, and 7 orders. Apparently *E. aedea* is polyphagous and not confined to tea, *Camellia sinensis*. Although the main purpose of the present study is not to evaluate the pest status of this species in different countries, it is necessary to emphasize that different subspecies seem to have

Fig. 4. Distribution map of all the presently recognized subspecies of *Eterusia aedea*. Data of geographical distribution based on Endo and Kishida (1999), Horie et al. (2000), Owada (2001), and material examined in the present study.

different host ranges, which may be significant for integrated pest management. Of all the subspecies, only *aedea*, *sinica*, *formosana*, *cingala*, and *virescens* have been reported as pests, and none of the subspecies in the Japanese archipelago has been considered a pest. It would be desirable to verify if host plant literature records are based on field observations, tests in the laboratory, or represent host plant shifts with development or with food resource availability after hibernation.

Context of research on *Eterusia aedea*

Eterusia aedea is possibly the most significant species among the Chalcosiinae because its pest status, commonness, and size have allowed scientists to address various questions not only about this species, but also about the family and superfamily. Long-term research by Owada and his colleagues has provided an excellent basis for future studies. I am particularly interested in several aspects. The high differentiation and distribution pattern of this species on the Japanese archipelago, Taiwan, and continental Asia can serve as a model study to reconstruct the biogeographical history of the East Asian I. Arc. As stated by Owada (1989 2001), Nishihara (1995), and Endo and Kishida (1999), phenology varies with different subspecies, providing an opportunity to evaluate if phenology is influenced by climatic differences, or the quality and availability of host plant resources.

The evolution of the wing patterns in *E. aedea* has long amazed scientists; however, the mechanisms of how insular subspecies have evolved more-monotypic wing patterns and why the continental subspecies tend to be polymorphic are still unclear. The polymorphism of the nominotypical *aedea* has attracted great attention from many authors (e.g., Doubleday 1844, Walker 1854, Möschler 1872, Butler 1879 1881, Cotes and Swinhoe 1887, Hampson 1892, Kirby 1892, Swinhoe 1892, Dudgeon 1899, Pavie 1904, Jordan 1907-1908 1907-1909, de Salvaza 1919, Hering 1922, Tams 1924, Fletcher 1925, de Joannis 1928 [1930], Dufrane 1936, Lemée and Tams 1950, Owada 2001). On the basis of a study of museum collections and Owada's (2001) observations, intermediate types are present among the forms, and the presence of each color form is not correlated with geographical distribution. Owada and Ta (2002) even suspected that the "black form" (= *edocla*, *dulcis*, and *signata* forms) of *aedea* may form a mimicry complex joined by other *Eterusia*, Agaristine species, and cicadas.

Tarmann (1992b) discovered that in some genera of the Chalcosiinae the male scent organ, which is composed of a bundle of hairs arising from the hindwing base and which inserts into a pleural pouch in A2, is a potential synapomorphy of the subfamily. However, phylogenetic analyses by Yen (2003b c) have revealed that the scent organs of this subfamily are much more complex and not only present in the males. At least 9 different combinations among different character states of the hindwing scales/hairs and pleural modifications have been defined (Yen 2003c). According to my preliminary observation of the courtship behaviors of *Chalcosia diana* Butler, 1877 and *Aglaope infausta* (Linnaeus, 1767), the male may flutter the wings quickly to draw the hairs from the pleural pouch, and thus the pheromone excreted by the glandular cells within the pleural pouch can be released to attract the female. This behavior has never been observed in the clade that includes *Eterusia* and related genera because they all lack the hindwing hairs and have a strongly sclerotized pouch which cannot be everted during courtship. This type of scent organ has been discovered not only in the *Eterusia* genus-complex but also in other unrelated lineages. So *E. aedea* may be the best model to investigate how courtship proceeds without androconial hairs, and why the pleural pouches are heavily sclerotized in both sexes.

Finally, the copulatory mechanism in the Zygaenidae has only been studied in *Zygaena trifolii* (Fänger and Naumann 1998), a species which demonstrates the typical genitalia and associated musculature of the higher ditrysian Lepidoptera, while copulation in the terminal clades of Chalcosiinae is greatly assisted by the specialized 8th abdominal segment (Yen 2003b c). Since many of the main parts of the male genitalia, considered to serve the function of holding the female abdomen, are greatly reduced, the fork-like tergite and the valva-like sternite are supposed to replace the function and morphology of the reduced uncus and valvae. The large size of *E. aedea* makes research on the copulatory mechanism possible, and the results can be used to infer the mechanism in other chalcosiine clades which have similar evolutionary trends in copulatory structures.

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Appendix I: A checklist of the valid subspecies of *Eterusia aedea*

In this appendix, the valid and available names, original generic placement (in brackets), type locality (country or area in brackets) and type depository of each taxon are provided. The name of the type locality follows the spelling in the original literature. "§" denotes that the taxon was described from illustrations. "※" denotes that the type depository of the taxon is uncertain. For the full names of institutions see "Materials and Methods".

Eterusia aedea aedea (Linnaeus, 1763) (*Papilio* (*Heliconius*)), "India", §
  Heterusia edocla Doubleday, 1844, **syn. nov.**, Sylhet (Bangladesh), BMNH (Note)
  Heterusia dulcis Butler, 1881, **syn. nov.**, Darjeeling (India), BMNH
  Heterusia signata Möschler, 1872, **syn. nov.**, India, ZMHB
  Eterusia magnifica Butler, 1879, **syn. nov.**, Cachar (India), BMNH
  Eterusia adocla [sic] form *lepcha* Jordan, 1907, **syn. nov.**, Myanmar, BMNH
Eterusia aedea sinica Ménétriés, 1857, **stat. rev., comb. nov.,** China, ZIN?
Eterusia aedea cingala Moore, 1877, Sri Lanka, BMNH
  Heterusia aedea var. *septentrionicola* C. Felder et R. Felder, 1862, Ceylan, ※
Eterusia aedea virescens (Butler, 1881) (*Heterusia*), Khandala (S. India), BMNH
Eterusia aedea formosana Jordan, 1907, Taiwan, BMNH
  Eterusia aedea ab. *postlutea* Strand, 1916, Alikang (Taiwan), DEI
Eterusia aedea sugitanii Matsumura, 1927, Nara, Honshu (Japan), HUFA
  Eterusia aedea okinoshimensis Esaki et Inoue, 1956 (*Eterusia*), Okinoshima (Japan), ELKU
Eterusia aedea micromaculata Inoue, 1982, Tokara Islands (Japan), BMNH
Eterusia aedea tomokunii Owada, 1989, Amami-oshima (Japan), NSMT
Eterusia aedea sakaguchii Matsumura, 1927, Okinawa Island (Japan), HUFA
Eterusia aedea okinawana Matsumura, 1931, Ishigaki Island (Japan), HUFA,
  Eterusia aedea ab. *okinawana* Matsumura, 1927, unavailable name
  Eterusia aedea ishigakiana Inoue, 1982, Ishigaki Island (Japan), BMNH
Eterusia aedea masatakasatoi Owada, 2001, Nakanoshima Island (Japan), NSMT
Eterusia aedea hamajii Owada, 2001, Tokunoshima Island (Japan), NSMT
Eterusia aedea azumai Owada, 2001, Kumejima Island (Japan), NSMT

Note: Year of publication of *edocla* has been misquoted as 1847 since Bryk (1936).

Appendix II: Collection data of the *Eterusia aedea* specimens examined

Eterusia aedea aedea (Linnaeus, 1863)
"black form" (=*edocla*, *dulcis*, *signata*)
Myanmar: 1♀, Karen Hils, 15-20 June 1916 (collector unknown); 2♂♂2♀♀, Bhamo, 1-2, May, 1916; 2♂♂1♀, Myamyo, 17 April 1901 (H.J.W. Barrow). Bhutan: 3♂♂1♀, Buxa (data and collector unknown). Vietnam: 1♂, Cochin China, Ko-Tich, Auguest 1935 (S. Masseyeff); 2♂♂, Tonkin, 1919. India: 2♂♂4♀♀, Khasis (ex Nat[ative] Coll[ector]); 3♂♂5♀♀, Khasia Hills, Assam, 1883 (W.A. Hamilton); 2♂♂3♀♀, Darjeeling (ex Moore Coll.); 3♂♂4♀♀, Gopaldhara, Darjeeling (H. Stevens). Thailand: 1♂, Chiang Mai, April 1921 (E.J. Godfrey). China: 2♂♂, Hainan, 1929 (data and collector unknown).

"yellow form" (=*magnifica*)
India: 8♂♂11♀♀, Assam, Shillong; 7♂♂2♀♀, Sikkim, Darjeeling, 1894 (R.P. Breiaudeau); 2♂♂2♀♀, Gopaldhara, Darjeeling (H. Stevens). Vietnam: 2♂♂, Cochin China, May 1936 (S.M. Masseyeff). Bhutan: 2♂♂2♀♀, Buxa (data and collector unknown). Myanmar: 2♂♂, Shan States, June-August 1902 (Hauxwell).

"white form" (=*lepcha*)
India: 4♂♂1♀, Khasia [Hills], November 1894 (ex. Nat[ive] Coll[ector]); 4♂♂, Khasia Hills, 1883 (W.A. Hamilton); 1♂, Cherrapunji, April, 1899 (collector unknown); 3♀♀, Shillong (data and collector unknown). Myanmar: 1♂, Burma (data and collector unknown); 2♂♂, Shan States, Hsipow (data and collector unknown).

Eterusia aedea sinica Ménétriés, 1857
China: 1♂2♀♀, [Jiangxi Province], Kiukiang, June 1887 (A.E. Pratt) (ex Leech Coll. 1900-64); 1♂, [Sichuan Province], Chin-Fu-Shan, W. China, date unknown (W.A. Maw); 5♂♂2♀♀, Omeishan, June & July 1890 (ex. Nat[ive] Coll[ector]); 1♂, Chia-Tin-Fu, July 1899 (A.E. Pratt); 6♂♂, Tatsienlou, 1892 (ex. Nat[ive] Coll[ector]); [Zhejiang Province], 1♂1♀, Chusna Island, June 1892 (ex. Walker Coll.); 2♂♂2♀♀, Wenchow (C.T. Bouwing); 1♀, [Fujien Province], Fo-kien, Ting-hai, May 1899 (P. de la. Garde.); 1♀, [Gueizhou Province], Kouy-Tcheou (A. Largeteau); 2♂♂2♀♀, Kwei-chow, June-July, 1890 (ex. Nat[ive] Coll[ector]); 2♂♂2♀♀, [Hunan Province], Hunan, C. China (A.E. Pratt); 4♂♂5♀♀, [Hubei Province], Chang-Yang, 1889 (native collector); 2♂♂2♀♀, Tibet, 1905 (P. Dejean); [Guangxi Province], 1♀, Nan-ning-fu (data and collector unknown).

Eterusia aedea formosana Jordan, 1907
Taiwan: 2♂♂, I-Lan, Yuanshan, Fushan Botanical Garden, 22 September 1996 (S.H. Yen); 1♂, Tainan, Kanshirei (=Kuantziling), 30 June 1908 (A.E. Wileman); 3♂♂, Chiayi, Koannia, September 1906 (A.E. Wileman).

Eterusia aedea okinawana Matsumura, 1931
Japan; 4♂♂1♀♀, Ishigaki, September-October 1890.

All specimens in BMNH.

Appendix III: Hostplants of *Eterusia aedea*, ordered according to the plant classification proposed by Judd et al. (1999)

Hostplant	Subspecies name	Collection source	References
ORDER Malpighiales			
Family Euphorbiaceae			
Bischofia javanica	*Eterusia aedea formosana*	Taiwan	SHY
	Eterusia aedea okinawana	Ishigaki	Nishihara 2001
Aporosa lindleyana	*Eterusia aedea virescens*	S. India	Tremewan 1960
Aporosa villosa	*Eterusia aedea*	?	Tremewan 1960
ORDER Cornales			
Family Cornaceae			
Cornus florida	*Eterusia aedea okinawana*	Ishigaki	Nishihara 2001
ORDER Myrtales			
Family Lythraceae			
Largerstroemia sp.	*Eterusia aedea aedea*	N. India	Sevastopulo 1940 1947
	Eterusia aedea cingala	Sri Lanka	Moore 1882 [1880-1887]
Family			
Melastoma candidum	*Eterusia aedea okinawana*	Iriomote	SHY
	Eterusia aedea okinawana	Ishigaki	Nishihara 2001
ORDER Fagales			
Family Myricaceae			
Myrica rubra	*Eterusia aedea okinawana*	Ishigaki	Nishihara 2001
ORDER Malvales			
Family Elaeocarpaceae			
Sloanea formosana	*Eterusia aedea formosana*	Taiwan	SHY
ORDER Ericales			
Family Ericaceae			
Rhododendron sp.	*Eterusia aedea sugitanii*	Japan	Nishihara 1995
	Eterusia aedea formosana	Taiwan	SHY
	Eterusia aedea okinawana	Ishigaki	Nishihara 2001
Family Symplocaceae			
Symplocos glauca	*Eterusia aedea sugitanii*	Honshu	Nishihara 1992
Family Theaceae			
Camellia sp.	*Eterusia aedea virescens*	S. India	Fletcher 1914, Tremewan, 1960
	Eterusia aedea aedea	N. India	Sevastopulo 1947 1949
	Eterusia aedea formosana	Taiwan	Sonan 1933, Wang 1999
	Eterusia aedea cingala	Sri Lanka	Moore 1882 [1880-1887], Gardner, 1942
Camellia japonica	*Eterusia aedea aedea*	N. India	Tremewan 1960, Tarmann 1992a
	Eterusia aedea okinawana	Ishigaki	Nishihara 1992, Murase 1993
	Eterusia aedea okinawana	Yonaguni	Murase 1995
	Eterusia aedea sugitanii	Honshu	Okuno 1952
	Eterusia aedea azumai	Kumejima	Owada 1995
Camellia sasanqua	*Eterusia aedea okinawana*	Ishigaki	Nishihara 1992
Camellia sinensis	*Eterusia aedea sinica*	C. China	Zhu et al. 1979, Wang 1983, Yang and Hu 1987
	Eterusia aedea aedea	N. India	Robinson et al.
Camellia oleifera	*Eterusia aedea sinica*	C. China	Wang 1983
	Eterusia aedea formosana	Taiwan	SHY
Family			
Eurya japonica	*Eterusia aedea aedea*	N. India	Tremewan 1960
	Eterusia aedea sugitanii	Honshu	Okuno 1952, Nishihara 1992
Eurya septata	*Eterusia aedea formosana*	Taiwan	SHY
Cleyera japonica	*Eterusia aedea sugitanii*	Honshu	Nishihara 1992
ORDER Lamiales			
Family Buddlejaceae			
Buddleja sp.	*Eterusia aedea aedea*	N. India	Mathur et al. 1958

SHY: First reported in the present study based on my unpublished data.